TRIASSIC VERTEBRATE PALEONTOLOGY IN NEW MEXICO

By: **Andrew B. Heckert** and Spencer G. Lucas

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TRIASSIC VERTEBRATE PALEONTOLOGY IN NEW MEXICO

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Abstract—The Triassic vertebrate paleontological record of New Mexico includes important assemblages of tetrapod fossils from both the Middle Triassic Moenkopi Formation and the Upper Triassic Chinle Group. The Anton Chico Member of the Moenkopi Formation preserves primarily temnospondyl amphibian body fossils, but the record of reptiles comprises both sparse body fossil assemblages and more abundant track assemblages, mostly of chirotheriid reptiles. A bonebed accumulation of temnospondyls assigned to *Eocyclotosaurus appetolatus* is particularly notable. The Upper Triassic Chinle Group in New Mexico preserves an array of vertebrate faunal assemblages that represent the entirety of Chinle "time," and includes numerous bonebeds of Revueltian age as well as the best records of Apachean vertebrates in the American West. These include the characteristic assemblages of the Revueltian and Apachean land-vertebrate faunachrons.

INTRODUCTION

The Triassic of New Mexico is world-famous, not only for the extensive collecting history dating to the 1870s, but also because of the important Lagerstätten, including the famous Whitaker (*Coelophysis*) quarry and Lamy amphibian quarry, specimens of which (Fig. 1) are iconic representatives of Upper Triassic taxa and are on display in museums around the world. Researchers representing numerous institutions across the United States have collected and published on Triassic vertebrate fossils from New Mexico, dating back to E.D. Cope (1875a,b). Consequently, collections of Upper Triassic fossils from New Mexico are spread across the country. Historically, the vast majority of these have been from the Upper Triassic Chinle Group; the Moenkopi Formation in New Mexico has only relatively recently received extensive study, and almost all Moenkopi Formation vertebrate fossils from New Mexico are housed at the New Mexico Museum of Natural History and Science (NMMNH).

Especially large collections of Chinle vertebrates from New Mexico are housed outside the state at the American Museum of Natural History (AMNH), the University of California Museum of Paleontology (UCMP), and the Carnegie Museum of Natural History (CMNH), but other collections include the Denver Museum of Nature and Science (DMNH), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University (MCZ), Museum of Northern Arizona (MNA), National Museum of Natural History (Smithsonian—USNM), State Museum of Pennsylvania (SMP), University of Colorado Museum (UCM), University of Michigan Museum of Paleontology (UMMP), and Yale Peabody Museum (YPM). Additionally, CMNH expeditions to Ghost Ranch in the 1980s resulted in the collection of numerous blocks from the famous Whitaker (*Coelophysis*) quarry going to museums across the country (including many of the museums listed previously) and also to the Royal Tyrell Museum in Drumheller, Canada (Colbert, 1989; Rinehart et al., 2009).

Hunt and Lucas (1993a) previously reviewed the Triassic vertebrate record of New Mexico, with Heckert et al. (2000a) updating the dinosaurian records. Heckert (2005) provided another overview as part of the 2005 "digital reprinting" of *Dawn of the Age of Dinosaurs in the American Southwest* (Lucas and Hunt, 1989). Since the review of Hunt and Lucas (1993a), more than 20 new vertebrate taxa have been named from Triassic strata in New Mexico (Table 1), and many other taxa named elsewhere have been identified in New Mexico. Beginning in the 1980s, concentrated efforts by the NMMNH have led to extensive collections of both Chinle and Moenkopi vertebrates that have stayed in state, and many of the more spectacular and/or significant fossils from those excavations are now on display in the Triassic hall at the NMMNH, which also motivated new reconstructions and restorations of many taxa (e.g., Fig. 2). Other institutions in the state, including the Mesalands Dinosaur Museum (MDM) in Tucumcari and the Ruth Hall Museum of Paleontology (RHMP) at Ghost Ranch in Abiquiu have also developed collections and exhibits of New Mexico's Triassic vertebrates during the last two decades.

Beyond museum collections, New Mexican Triassic fossils are well represented in synthetic taxonomic works (e.g., Long and Murry, 1995; Fraser, 2006; Sues and Fraser, 2010; Nesbitt, 2011). As an example, the recent archosaur volume (Nesbitt et al., 2013), with its systematic reviews of doswelliids (Sues et al., 2013), phytosaurs (Stocker and Butler, 2013), aetosaurs (Desojo et al., 2013), rauisuchians (Nesbitt et al., 2013), crocodylomorphs (Irmis et al., 2013), and dinosauromorphs (Langer et al., 2013), draws heavily on the Triassic vertebrate fossil record of New Mexico.

The New Mexican Triassic record is stratigraphically complex. Unlike some of the younger fossiliferous strata in the state, such as the Cretaceous (Sullivan and Lucas, 2015) and Paleogene (Kondrashov and Lucas, this volume) of the San Juan Basin, Triassic System strata crop out across numerous distinct outcrop belts (Fig. 3), many of which bear their own internal stratigraphy (Fig. 4; Lucas, 2004). All Middle Triassic strata are easily correlated as the Anton Chico Member of the Moenkopi Formation. The Upper Triassic strata were all deposited along the axis of a northwesterly flowing river system in the Chinle basin (e.g., Lucas, 1993, 1997). Stratigraphic units from different outcrop belts record distinct aspects of Chinle deposition, requiring us to divide our discussion both geographically (Fig. 3) and stratigraphically (Fig. 4; Tables 2–4).

We note that the information presented herein is an overview—for details of specimen numbers, localities, specific stratigraphic positions, and so on, the reader is referred to the primary literature cited herein. A previous review (Heckert et al., 2005a), though on a smaller scale, was criticized extensively by Nesbitt and Stocker (2008) for failing to provide apomorphy-based justifications of the assignments it contained. We regard an apomorphy-based approach as problematic (e.g., Heckert et al., 2012b), and the purpose of this paper is to provide as nearly as possible a comprehensive review of what is known so that the interested reader has a synthesis in hand, together with ready access to a list of the relevant literature on which that synthesis is based. To exhaustively document the thousands of cataloged, Triassic vertebrate fossils from New Mexico housed at the NMMNH alone, let alone the historic collections listed previously, is well beyond the scope of this review.

VERTEBRATE PALEONTOLOGY OF THE MOENKOPI FORMATION IN NEW MEXICO

Introduction

The presence of Moenkopi strata in New Mexico had only been confirmed less than a decade before Hunt and Lucas' (1993a) review (e.g., Lucas and Morales, 1985; Lucas and Hunt, 1987), and these deposits have received much paleontological attention during the last two decades, summarized in part by Boy et al. (2001) and Schoch et al. (2010). These are strata of the upper part of the Moenkopi lithosome, the Anton Chico Member of the Moenkopi Formation (Lucas and Hunt, 1987). These youngest Moenkopi strata are the only Middle Triassic portion of the lithosome and are correlative to the Holbrook Member of the Moenkopi Formation in northern Arizona (Lucas and Schoch, 2002). In northeastern New Mexico, these strata may be in part correlative with the Jelm Formation, which has been recognized in the Picketwire Grasslands in southeastern Colorado (Heckert et al., 2012c).

The most extensive collections of Moenkopi vertebrate fossils from New Mexico come from a suite of localities in the Pecos River drainage in San Miguel and Guadalupe counties in east-central New

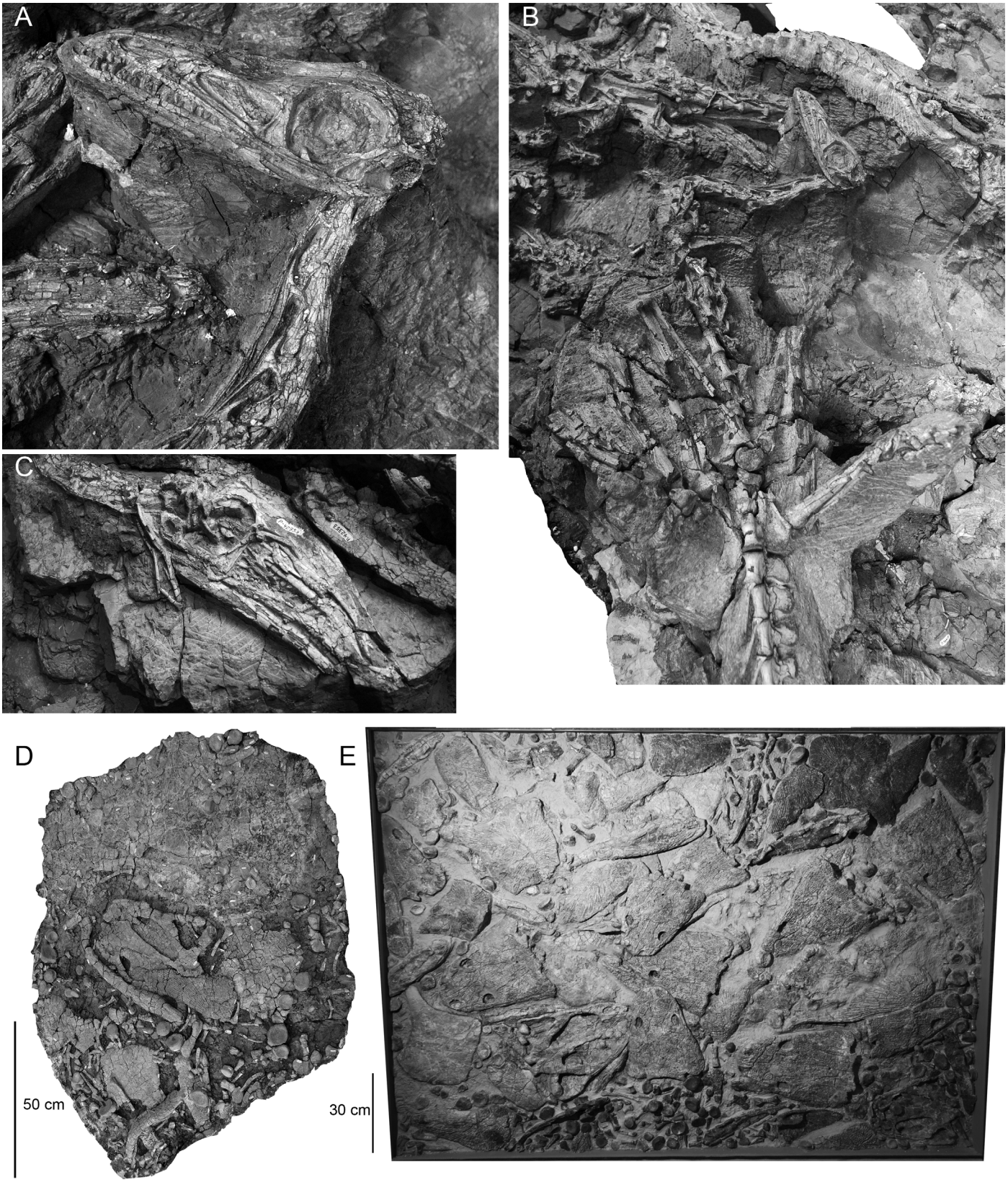

FIGURE 1. Representative specimens of iconic bonebeds from the Upper Triassic of New Mexico. **A–C**, specimens of *Coelophysis bauri* from the NMMNH block from the Whitaker quarry; **A**, juvenile skull of *Coelophysis bauri*; **B**, articulated skeleton of the same specimen; **C**, skull of *Coelophysis bauri*; **D–E**, numerous bones of the metoposaurid amphibian *Koskinonodon* from the Lamy amphibian quarry; **D**, NMMNH block from the Lamy amphibian quarry; and **E**, the MCZ block from the Lamy amphibian quarry as mounted outside of Romer's Harvard office.

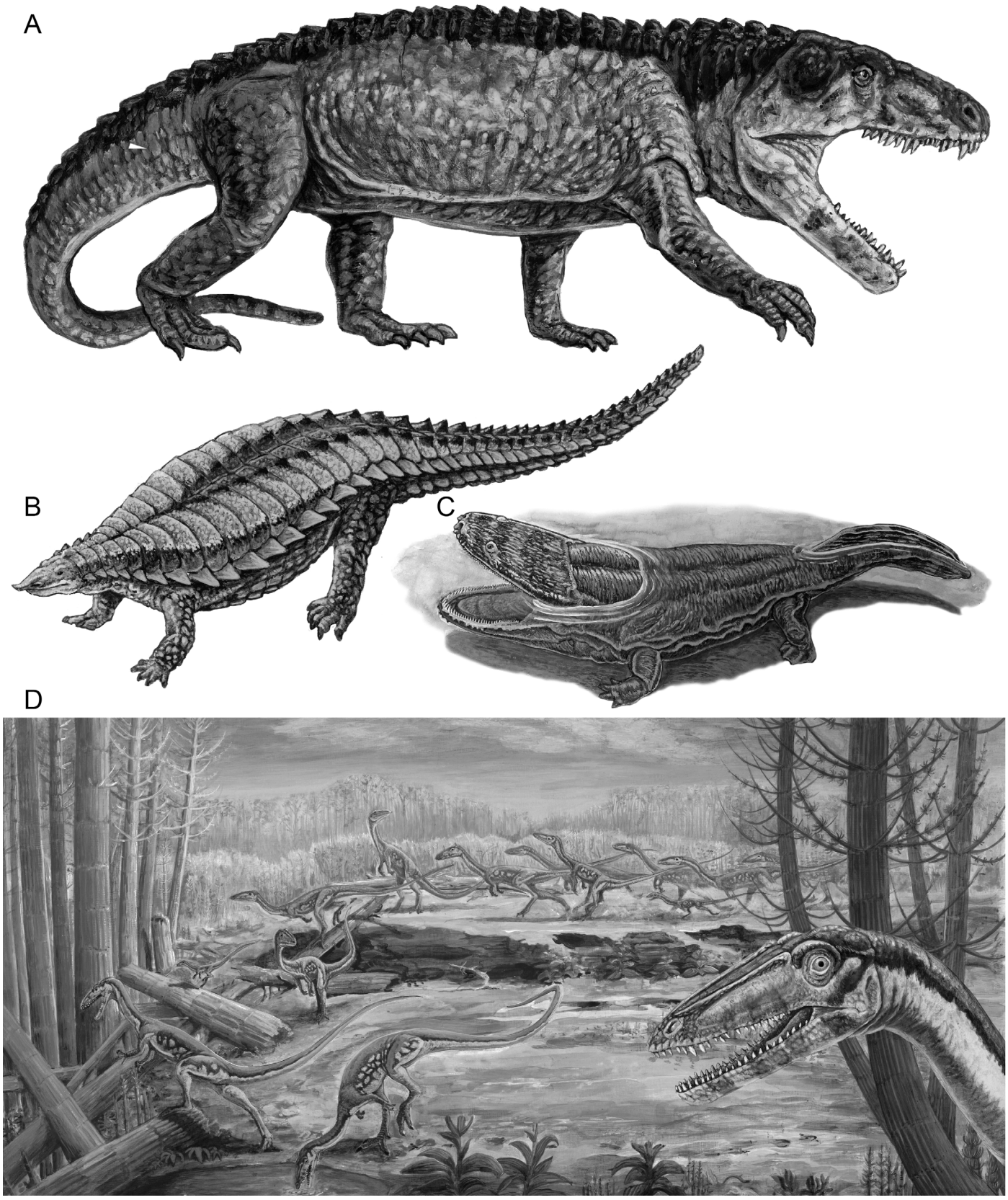

FIGURE 2. Life restorations of selected Triassic tetrapods from New Mexico. **A**, the erythrosuchian from the Moenkopi Formation; **B**, the aetosaur *Typothorax coccinarum*; **C**, the metoposaurid amphibian *Koskinonodon*; and **D**, the theropod *Coelophysis bauri* in the landscape represented by the Rock Point Formation. All restorations by Matt Celeskey; individual restorations are not to scale with each other.

TABLE 1. New vertebrate taxa named from the Triassic of New Mexico, 1993–2015.

Osteichthyes: Coelacanthidae
Quayia zideki Hunt 1997a
Temnospondyli: Metoposauridae
Apachesaurus gregorii Hunt 1993
Eocyclotosaurus appetolatus Rinehart et al. 2015
Lepidosauria: Sphenodontia
Whitakersaurus bermani Heckert et al. 2008
Archosauriformes *incertae sedis*
Doswellia sixmilensis Heckert et al. 2012a
Lucianosaurus wildi Hunt and Lucas 1994
Archosauriformes: Phytosauria
Redondasaurus gregorii Hunt and Lucas, 1993c
Redondasaurus bermani Hunt and Lucas, 1993c
Archosauria: Suchia *incertae sedis*
Krzyzanowskisaurus (=*Revueltosaurus*) *hunti* (Heckert) 2002 (see Heckert, 2005; Heckert and Miller-Camp, 2013)
Suchia: Stagonolepididae
Apachesuchus heckerti Spielmann and Lucas 2012
Redondasuchus rineharti Spielmann et al. 2006
Rioarribasuchus (=*Desmatosuchus*) *chamaensis* (Zeigler et al.) 2002; see Lucas et al. (2006b)
Typothorax antiquum Lucas et al. 2002a
Archosauria: Suchia: Paracrocodylomorpha
Effigia okeeffeae Nesbitt and Norell 2006; see Lucas et al. (2007b)
Archosauria: Suchia: Sphenosuchia
Redondavenator quayensis Nesbitt et al. 2005
Archosauria: Dinosauriformes
Dromomeron romeri Irmis et al. 2007a
Eucoelophysis baldwini Sullivan and Lucas 1999
Tawa hallae Nesbitt et al. 2009a
Dinosauria: Theropoda
Daemonosaurus chauliodus Sues et al. 2011
Gojirasaurus quayi Carpenter 1997
Testudines
Chinlechelys tenertesta Joyce et al. 2009
Synapsida: Cynodontia
Redondagnathus hunti Spielmann and Lucas 2012
Ichnofossils
Apachepus cottonorum Hunt and Lucas 2007
Barrancapus cresapi Hunt et al. 1993

Mexico (Fig. 3), but other, fragmentary fossils have been recovered from numerous sites, including the Lucero uplift (Lucas and Hayden, 1989) and near Carthage in Socorro County (Spielmann and Lucas, 2009). The most extensive Moenkopi vertebrate-fossil locality in New Mexico is a bone bed (mass death assemblage) dominated by the capitosaurid amphibian *Eocyclotosaurus appetolatus* found near Tecolotito in Guadalupe County (Rinehart et al., 2010, 2015).

Moenkopi Formation Body Fossils

To date, the record of osteichthyans from the Moenkopi Formation of New Mexico is restricted to scales and other osseous materials in coprolites (Boy et al., 2001). Where Moenkopi tetrapods have been recovered in New Mexico, temnospondyls are locally abundant, and the most diagnostic specimens have been assigned to *Eocyclotosaurus* (Fig. 5) and cf. *Stanocephalosaurus* (e.g., Boy et al., 2001). Importantly, *Eocyclotosaurus* is an index fossil of Perovkan (Middle Triassic: Anisian) time, and the presence of *Eocyclotosaurus* in both the Moenkopi Formation and the Middle Triassic of Germany has facilitated correlation of the former to the global chronostratigraphic timescale (Lucas and Schoch, 2002; Lucas, 2010). More recently, Rinehart et al. (2013a,b, 2015) have used the New Mexico Moenkopi capitosauroid fossils as the basis for functional morphological analyses of dermal bone ornamentation and of tooth size and shape in temnospondyls.

The localities in the vicinity of the type section on the Anton Chico Land Grant have yielded numerous tetrapods, principally reptiles (Schoch et al., 2010). These include a procolophonoid and numerous archosauromorphs, including more derived archosauriforms, pseudosuchians, and poposauroids, such as the poposaurid *Arizonasaurus babbitti* and a shuvosauroid-like taxon. One of the more impressive reptilian discoveries is that of a large (6–7 m estimated body length), armored archosauriform from the vicinity of Tecolotito assigned to the Erythrosuchidae by Nesbitt et al. (2006), but which Schoch et al. (2010) more conservatively assigned to Archosauriformes indet.

Moenkopi Formation Trace Fossils

As would be expected, Moenkopi Formation tracksites in New Mexico are much less common than in the thicker and better exposed Moenkopi sections in Arizona and Utah, which were reviewed recently by Klein and Lucas (2010), so readers are referred to that publication for details of ichnotaxonomy and synonymy. Moenkopi tracksites in New Mexico are principally of chirotheriids and well fit the *Chirotherium barthii* zone (Nonesian–Perovkan land vertebrate faunachron [lvf]) of Olenekian to Anisian age. Here, we simply note that tracksites from New Mexico not covered by Klein and Lucas (2010) have been discovered, including the Zuni Mountains tracksites near Bluewater (Lucas and Hayden, 1989; Hunt and Lucas, 1993d; Lucas et al., 2003a). Other vertebrate trace fossils from the Moenkopi Formation are limited to coprolites, which co-occur with fossil bones at numerous localities (Boy et al., 2001). Hunt and Lucas (2015) provide a more detailed review of New Mexican Moenkopi traces elsewhere in this volume.

VERTEBRATE PALEONTOLOGY OF THE CHINLE GROUP IN NEW MEXICO

Introduction

Due to the complexity and extent of the Upper Triassic vertebrate record in the Chinle Group of New Mexico, we have divided our discussion into a section on body fossils (principally bones and teeth) and a brief section on trace fossils (principally footprints and coprolites). Again, the trace fossil record (including coprolites) is covered in more detail by Hunt and Lucas (2015) in this volume. The body fossil discussion is further broken down by region and stratigraphic horizon.

Chinle Group Body Fossils

The Chinle Group crops out across numerous belts, crossing major physiographic and tectonic boundaries (e.g., Colorado Plateau, Rio

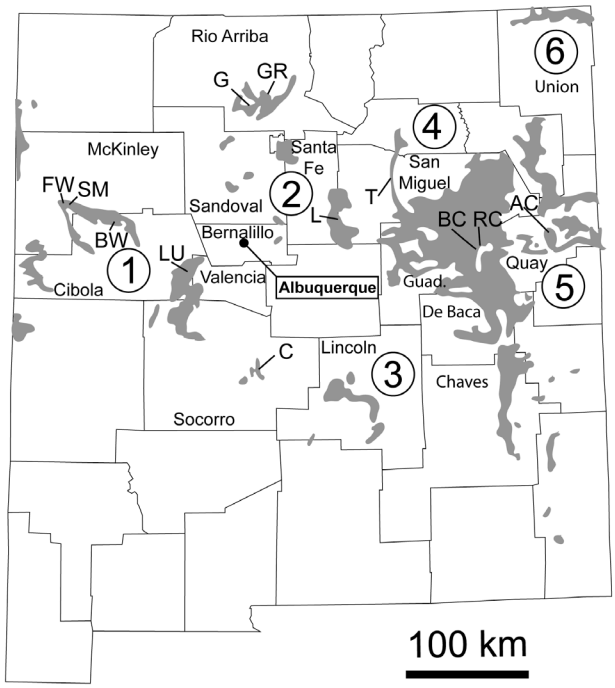

FIGURE 3. Map showing Triassic outcrop belts in New Mexico. Large numbers refer to stratigraphic terminology in columns in Figure 4. Letters refer to the following localities: AC = Apache Canyon; BC = Barranca Creek; BW = Bluewater; C = Carthage area; FW = Fort Wingate; G = Gallina; GR = Ghost Ranch; L = Lamy; RC = Revuelto Creek; SM = Six Mile Canyon; T = Tecolotito.

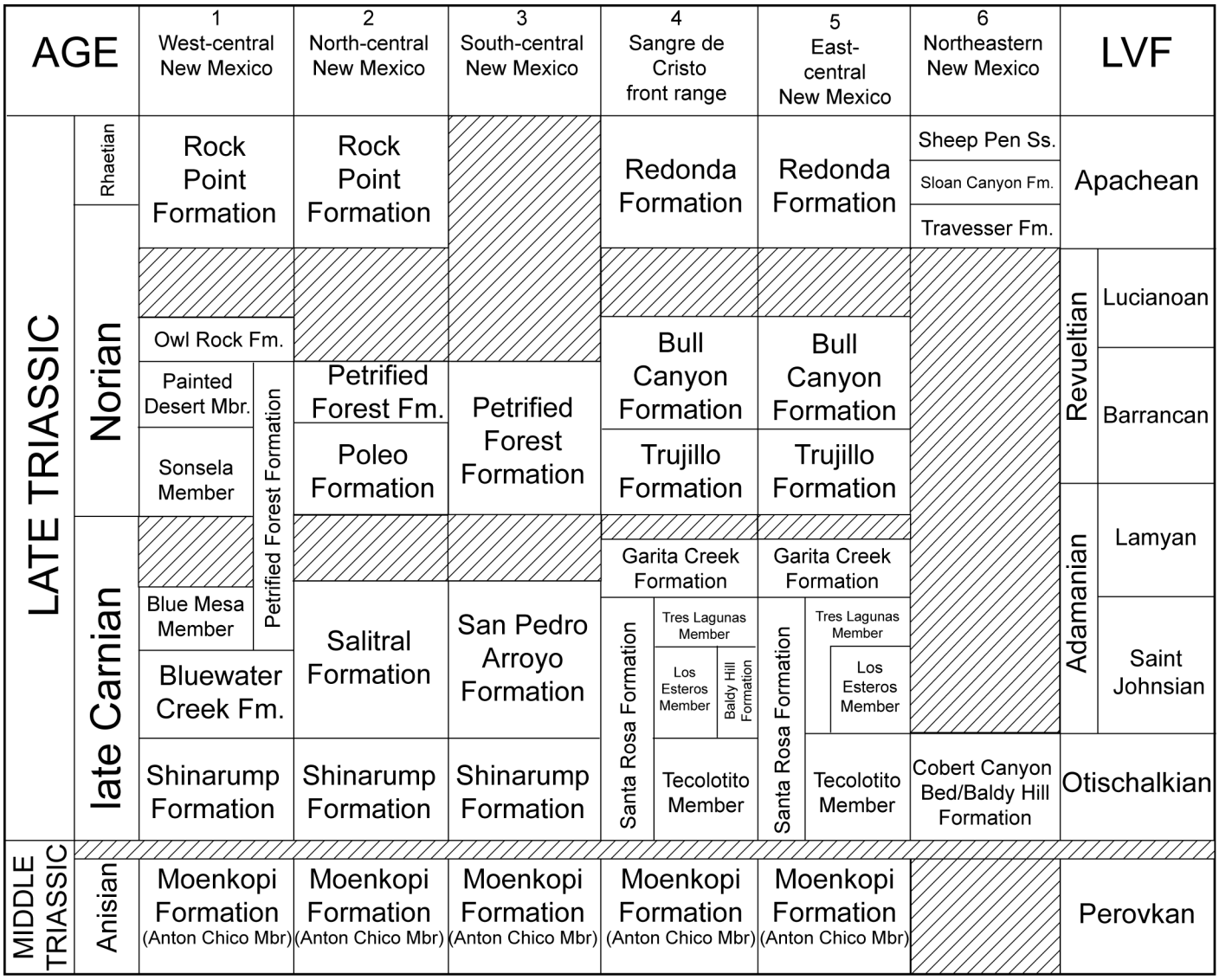

FIGURE 4. Correlation of Triassic strata in New Mexico (modified from Lucas, 2004). See Figure 3 for outcrop map.

Grande rift, High Plains), which has resulted in a complex history of stratigraphic nomenclature based more on modern outcrop distribution than on the unity of the original deposits during the Late Triassic (Lucas, 1993, 1997, 2004). We therefore arbitrarily cover this record from west to east, describing the fossil record of the Zuni Mountains, north-central, south-central, east-central, and northeastern New Mexico (following Fig. 3).

Zuni Mountains

The Upper Triassic strata in the Zuni Mountains in west-central New Mexico have experienced intermittent paleontological reconnaissance since Mehl et al. (1916) reported fossils near Fort Wingate; the most recent reviews were published by Heckert (1997b, 2004) and Heckert and Lucas (2002c, 2003) as an outgrowth of Heckert's (1997a, 2001) thesis projects. The best assemblages are from the Bluewater Creek Formation, although other units have yielded fragmentary vertebrate fossils.

As reported by previous authors, the Bluewater Creek Formation in the Zuni Mountains area yields a typical Chinle Group tetrapod fossil assemblage of metoposaurid amphibians and a variety of archosaurs, principally phytosaurs and aetosaurs. The most productive and diverse localities are in the vicinity of Sixmile Canyon. Taxa diagnostic to lower taxonomic rank are rare, but include the aetosaurs *Stagonolepis* (=*Calyptosuchus*) *wellesi*, *Desmatosuchus haplocerus*, and *Tecovasuchus chatterjeei*, all index taxa of the Adamanian lvf (Lucas, 1998, 2010). The record of *Stagonolepis* is based in part on the (now lost) holotype of *Acompsosaurus wingatensis* Mehl et al. (1916), and Heckert et al. (2007b) reidentified an aetosaur osteoderm fragment as pertaining to *Tecovasuchus* for that record.

The diverse microvertebrate assemblage documented by Heckert (2004) comes from a similar, or slightly lower, stratigraphic horizon than the Sixmile Canyon assemblages in the lowermost Bluewater Creek Formation. Heckert (2004, table 11) documented that this assemblage includes xenacanth and hybodontoid chondrichthyans, redfieldiid, palaeoniscid, and coelacanthid osteichthyans, the metoposaurs *Koskinonodon* (=*Buettneria*) and *Apachesaurus*, diverse archosauromorphs, including aff. *Trilophosaurus jacobsi*, numerous archosauriform tooth morphotypes, phytosaurs, and possible dinosaurs, including the putative ornithischian *Crosbysaurus harrisae*. Irmis et al. (2007b) considered "ornithischians" such as *Crosbysaurus* as valid taxa, but diagnostic only of Archosauriformes *incertae sedis*. Regardless of its affinities, *Crosbysaurus* appears to be an index taxon of the Adamanian LVF (Heckert and Lucas, 2006)

Since the description of the microvertebrates by Heckert (2004), there have been several updates to the known fauna. Beatty and Heckert (2009) documented a large, pathological archosauriform tooth that could pertain to a phytosaur (as suggested by Heckert 1997a,b), but more likely represents a rauisuchian or other large archosaur from the same stratigraphic interval as the Sixmile Canyon assemblage. This interval also yielded the holotype of the archosauromorph *Doswellia sixmilensis* named by Heckert et al. (2012a).

Other Chinle stratigraphic units in the Zuni Mountains have not yielded as many or as identifiable vertebrate fossils. Heckert (1997a,b; see also Heckert and Lucas, 2002c, 2003) reported fragmentary

TABLE 2. Vertebrate faunal list of the lower Chinle Group in the Zuni Mountains (updated from Heckert, 1997a,b, 2001, 2004). Binomens with author names indicate type specimens.

Chondrichthyes
"*Xenacanthus*" sp.
Hybodontoidea indet.
Osteichthyes
Chinlea sp.
Redfieldiidae indet.
Palaeoniscidae indet. aff. *Turseodus*
Coelacanthidae indet.
Actinopterygii indet
Amphibia
Koskinonodon perfectum
Apachesaurus cf. *A. gregorii*
microvertebrate taxa
Primitive Reptiles: several microvertebrate taxa
Synapsida
Indeterminate ?dicynodont
Archosauriformes:
aff. *Trilophosaurus*
Crosbysaurus harrisae
Doswellia sixmilensis Heckert et al. 2012
Phytosauri
aff. *Angistorhinus* sp.
aff. *Rutiodon* sp.
Aetosauria
Desmatosuchus haplocerus
Calyptosuchus wellesi
Tecovasuchus chatterjeei
Dinosauromorpha
two theropods(?) of unknown affinities

assemblages of probable metoposaurs, phytosaurs, and aetosaurs from the Blue Mesa Member, which has more recently yielded several osteoderms of an aetosaurine aetosaur. The coarse-grained Sonsela Member lacks identifiable vertebrate fossils and does not appear to be as thick as it is farther to the west in the Petrified Forest National Park (Heckert and Lucas, 2002b), where it yields extensive vertebrate assemblages (Heckert et al., 2005b; Martz and Parker, 2010). Similarly, fragmentary fossils have been recovered from the Painted Desert Member, but much of its outcrop belt is poorly exposed and/or difficult to access. The Owl Rock Formation is well exposed along the northern flank of the Zuni Mountains, but is largely on Native American lands, which have more restricted access. Tiny outcrops of the Wingate Formation in the vicinity of Fort Wingate (e.g., Lucas and Anderson, 1998; Lucas et al., 2001a; Lucas, 2004) could be of Triassic age, but are unfossiliferous and are at least as likely to be earliest Jurassic as Triassic (Heckert and Lucas, 2003; Lucas and Tanner, 2007).

Northern New Mexico

The Chama Basin in northern New Mexico has yielded some of the state's most spectacular Triassic vertebrate fossils, with the most notable being the *Coelophysis*-dominated Whitaker quarry at Ghost Ranch. Since the review by Hunt and Lucas (1993a), major discoveries include the rich bonebeds of the Snyder and Hayden quarries, and numerous more isolated specimens. The best, and most fossiliferous, exposures of Triassic strata in the Chama Basin are in the younger part of the section (Petrified Forest and Rock Point formations), so we cover the stratigraphically lower units only briefly.

Shinarump, Salitral, and Poleo formations—The stratigraphically lowest Upper Triassic strata in the Chama Basin are referred to the Shinarump (= Agua Zarca) Formation. The strata are readily correlated to the homotaxial Shinarump and Zuni Mountains formations of west-central New Mexico (Lucas et al., 2003b, 2005; Zeigler et al., 2008), but are much thicker and appear to represent the local, axial Chinle drainage (e.g., Lupe and Siberling, 1985; Riggs et al., 1996). Only fragmentary fossils of phytosaurs, aetosaurs, and metoposaurs are known from the Shinarump Formation in the Chama Basin (e.g., Lucas et al., 2003b), none of which are age-diagnostic beyond Late Triassic .

In the Chama Basin, Salitral Formation strata are thin and do not crop out extensively, and thus have yielded only a fragmentary assemblage of "typical" Chinle vertebrates, essentially indeterminate metoposaurids (likely including *Apachesaurus* and *Koskinonodon* fossils), phytosaurs, and aetosaurs. The best assemblages were actually collected from the southern end of the Nacimiento uplift in Sandoval County on the southern side of the Jemez volcanic field, relatively far from the Chama Basin (Lucas and Hunt, 1992; Lucas and Heckert, 1996; Lucas et al., 2003b). An aetosaur osteoderm from this locality has been assigned to *Longosuchus* (Hunt and Lucas, 1990), *Desmatosuchus* (Lucas et al., 2003b), or ?Paratypothoracisinae (Parker and Martz, 2010).

Like the Shinarump Formation, the Poleo Formation is a coarse-grained unit composed primarily of channel sandstones. Thus, it, too, yields only fragmentary fossil vertebrates, including material of indeterminate temnospondyls (almost certainly metoposaurids) and phytosaurs.

Petrified Forest Formation—The Petrified Forest Formation interval in the Chama Basin hosts the vast majority of the Triassic vertebrate localities in northern New Mexico, including both the historic Canjilon and more recently discovered Snyder and Hayden quarries. Lucas et al. (2003b, 2005) divided the Petrified Forest Formation into a thin, sandstone-dominated, lower Mesa Montosa Member and a much thicker, mudstone-dominated, upper Painted Desert Member.

Mesa Montosa Member—The Mesa Montosa Member has yielded relatively few vertebrates, mostly those described by Zeigler et al. (2005b) and Stiegler and Zeigler (2006). Zeigler et al. (2005b) reported fragmentary fossils of indeterminate temnospondyls, the archosauriform *Vancleavea*, the phytosaur *Pseudopalatus*, the aetosaurs *Typothorax coccinarum* and *Paratypothorax*, a possible theropod, and putative fossils of a turtle (marginal osteoderms) and a pterosaur. The putative pterosaur fossil is almost certainly a drepanosaurid vertebra (compare Zeigler et al., 2005b, fig. 4a to Renesto et al., 2010, fig. 38a–d). Stiegler and Zeigler (2006) provided additional information on some of the phytosaur fossils from the Mesa Montosa Member.

Painted Desert Member—The overlying Painted Desert Member is the most fossiliferous unit in the Chama Basin Chinle section and host to the vast majority of the Triassic fossils in the area outside of the stratigraphically higher *Coelophysis* quarry. Numerous localities are known within the unit, and others are discovered regularly. Heckert et al. (2005a) summarized the various collecting areas, and the discussion here mirrors that terminology.

The most historic localities are those in the vicinity of Orphan Mesa, in the Arroyo Seco drainage, and near Gallina, on the western side of the basin (Fig. 3). Since Lucas and Hunt (1992), the primary interest in the Gallina area lies in the type materials of both *Coelophysis bauri* and *Typothorax coccinarum* (Lucas and Hunt, 1992; Heckert and Lucas, 2002d; Lucas et al., 2007a; Parker, 2013). The Orphan Mesa localities also include some of the collections of David Baldwin on which Cope (1881) based *Coelophysis* (Sullivan et al., 1996), as well as the type locality of the dinosauriform *Eucoelophysis baldwini* Sullivan and Lucas (1999; Ezcurra, 2006) and a variety of fossils at Ghost Ranch (Heckert et al., 2005a).

The holotype of the phytosaur "*Belodon*" *buceros* Cope (1881) is also from the Painted Desert Member, probably in the vicinity of Orphan Mesa ("Huerfano Camp" of Baldwin's correspondence to Cope—Lucas et al., 2002b). This taxon has subsequently been assigned to "*Metarhinus*" (Jaekel, 1910), *Machaeroprosopus* (Mehl, 1916), *Pseudopalatus* (Mehl, 1928), and *Arribasuchus* (Long and Murry, 1995). Parker et al. (2013) reviewed this complex taxonomic history and argued on nomenclatural grounds that Mehl (1916) did, in fact, assign the skull described by Cope to his (then-) new genus *Machaeroprosopus* and that therefore many of the phytosaur species assigned to these genera should be reassigned to *Machaeroprosopus*, a position followed by Stocker and Butler (2013) and Hungerbühler et al. (2013).

As noted by Heckert et al. (2005a), both Hunt and Downs (2002) and Martz (2002; Martz and Zeigler, 2005) independently reinvestigated the taphonomy of the Canjilon quarry, collected primarily by Charles Camp of the UCMP, but also intermittently by parties affiliated with Ghost Ranch. Nesbitt and Stocker (2008) determined that at least some of the aetosaur skeletons of *Typothorax* ascribed to the Canjilon quarry by Long and Murry (1995; see also Heckert et al., 2005a) in fact came from other, nearby localities, including Berberon Canyon, but were still collected from the Painted Desert Member at a comparable horizon. Lucas and Heckert (2011) used the hand and foot skeletons of these

TABLE 3. Vertebrate fauna of the Upper Triassic Petrified Forest and Rock Point formations of northern New Mexico. Binomens with author(s) indicate type specimens.

Petrified Forest Formation (updated from Heckert et al., 2005a)	**Rock Point Formation** (updated from Rinehart et al., 2009)
Chondrichthyes	
Lonchidion humblei P	
Chondrichthyes indet. P	
Osteichthyes	**Osteichthyes**
Palaeoniscidae indet. P	*Synoricthys* cf. *S. stewarti*
aff. *Turseodus* P	*Chinlea sorenseni*
Redfieldiidae indet. P	
Semionotidae indet. P	
Amphibia	
aff. *Koskinonodon*	
Temnospondyli indet.	
Synapsida	
Cynodontia indet. P	
Diapsida	**Diapsida**
Lepidosauromorpha indet. P	*Whitakersaurus bermani* Heckert et al. 2008
Archosauromorpha indet.	Archosauriformes indet.
Dolabrosaurus aquatilis Berman and Reisz 1992; P	*Vancleavea campi*
Archosauriformes indet.	*Drepanosaurus* sp.
Vancleavea campi P	
Drepanosauridae indet.	
Tanystropheidae indet.	
Crurotarsi	
Machaeroprosopus (=*Pseudopalatus*) *buceros* (Cope)	*Redondasaurus gregorii*
Phytosauridae indet.	
Stagonolepididae indet.	
Typothorax coccinarum Cope 1875	*Postosuchus kirkpatricki*
Rioarribasuchus chamaensis (Zeigler et al., 2002a); P	*Shuvosaurus* (=*Effigia*) *okeeffae* Nesbitt and Norell 2006
Paratypothorax sp.	*Hesperosuchus agilis*
Poposauridae indet.	
Shuvosauridae indet.	
Crocodylomorpha indet.	
Dinosauromorpha	
Eucoelophysis baldwini Sullivan and Lucas, 1999; P	*Eucoelophysis* sp.
Dromomeron romeri Irmis et al., 2007a; P	
Dinosauria	
Chindesaurus bryansmalli	
Tawa hallae Nesbitt et al., 2009a; P	*Coelophysis bauri*
Daemonosaurus chauliodus Sues et al., 2011	
Coelophysis sp. P	
Theropoda indet.	

M = restricted to Mesa Montosa Member; P = restricted to Painted Desert Member

Typothorax skeletons to bolster their appraisal of large aetosaurs as the likely trackmaker of the footprint ichnogenus *Brachychirotherium*.

The Snyder quarry is the richest single Triassic vertebrate locality in the Chama Basin from which collections reside solely at the NMMNH. Excavations began in 1998, were extensive in 1999–2001 (Heckert and Zeigler, 2003), and have continued intermittently in the years since then, with more than 100 jackets and hundreds of individual bones of fossils recovered. The assemblage from this quarry is both rich and diverse, with many exceptionally well preserved specimens (Zeigler et al., 2003a,b,e). These include microvertebrates (Jenkins, 2004; Heckert and Jenkins, 2005), numerous phytosaurs (Zeigler et al., 2002d, 2003c,d,e; Hurlburt et al., 2003), aetosaurs (Zeigler et al., 2002a; Heckert et al., 2003a), rauisuchians (Zeigler et al., 2003a,b,c) and theropod dinosaurs (Heckert et al., 2000b, 2003b; Nesbitt et al., 2007; Spielmann et al., 2007). This is the type locality of the aetosaur *Rioarribasuchus chamaenesis* (Zeigler et al., 2002a; Heckert et al., 2003a; Lucas et al., 2006a; Parker, 2007). The sedimentology and taphonomy of the site have been investigated in great detail (Zeigler et al., 2002b; 2005b; Tanner et al., 2003; Zeigler, 2003); where those references disagree, we favor the interpretations of Tanner et al. (2003), namely that the assemblage formed as the result of the accumulation of a large number of carcasses and charcoal in a hyperconcentrated flow of intraformational material reworked from the adjoining floodplain after a significant wildfire event. The available evidence is ambiguous as to whether the fire was directly related to the mortality event (Tanner et al., 2003; Zeigler et al., 2003), although it is certainly possible. The consensus fauna thus consists of the hybodont *Lonchidion humblei*, semionotid and redfieldiid osteichthyans, temnospondyls, a cynodont, a lepidosauromorph, numerous phytosaurs assigned to *Machaeroprosopus* (=*Pseudopalatus*) *buceros*, the aetosaurs *Typothorax coccinarum*, *Rioarribasuchus chamaensis*, and ?*Paratypothorax*, a *Postosuchus*-like rauisuchian, and the coelophysoid theropod *Coelophysis*.

The Hayden quarry was discovered shortly after the Snyder quarry, and has been the focus of excavations for most, if not all, field seasons at Ghost Ranch since 2001. Although we await a synthetic volume, key discoveries thus far include the dinosauromorph *Dromomeron romeri* Irmis et al. (2007a), a ?silesaurid, and the theropod *Tawa hallae* (Nesbitt et al., 2009a). Irmis et al. (2011) reported an age of ~212 Ma for the Hayden quarry based on U-Pb dates from detrital zircons. Other taxa from the quarry reported by these authors include indeterminate metoposaurids, a tanystropheid (Pritchard et al., 2015), a drepanosaur, *Vancleavea*, the phytosaur *Machaeroprosopus*, the aetosaurs *Typothorax coccinarum* and *Rioarribasuchus chamaensis*, indeterminate rauisuchians, including a "*Shuvosaurus*-like" taxon, a crocodylomorph, the theropod *Chindesaurus bryansmalli*, and indeterminate coelophysoids.

Shortly before the Hunt and Lucas (1993a) review, Berman and Reisz (1992) named the enigmatic reptile *Dolabrosaurus aquatilis* (Berman and Reisz, 1992) and indicated that it was perhaps from the Rock Point Formation. *Dolabrosaurus* is now clearly a drepanosaurid,

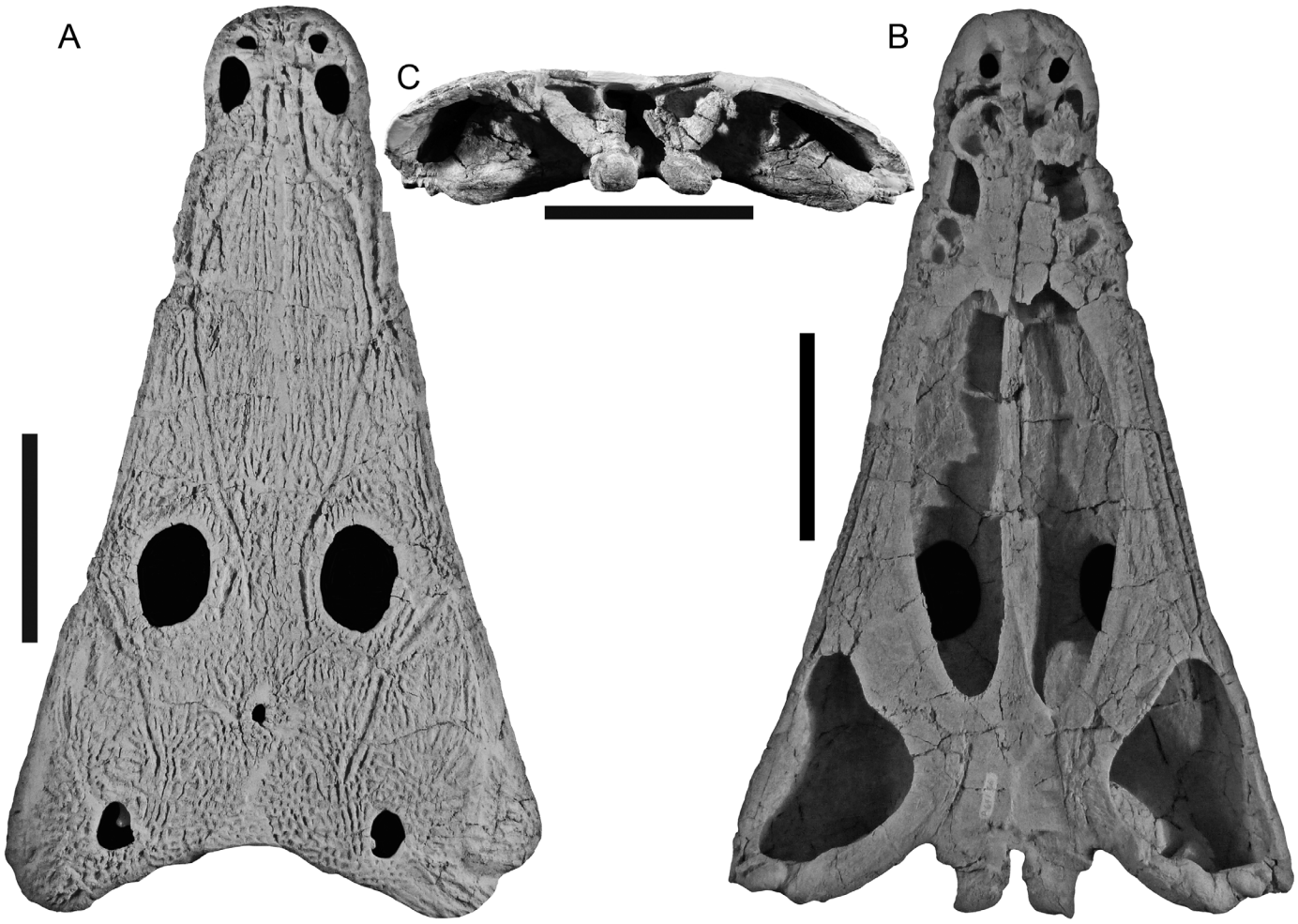

FIGURE 5. Holotype skull (NMMNH P-64166) of *Eocyclotosaurus appetolatus* from NMMNH locality 5193, the Anton Chico bonebed in **A**, dorsal, **B**, ventral, and **C**, posterior views.

and Renesto et al. (2010) established that the type locality is, in fact, from the lower Painted Desert Member in the Chama basin.

Rock Point Formation—The bulk of the known fossil record from the Rock Point Formation in the Chama Basin comes from the Whitaker (*Coelophysis*) quarry. Other sites have been discovered, but the fossils from these remain largely unpublished. AMNH blocks excavated under the direction of E.H. Colbert in the 1940s and CMNH blocks excavated in the early 1980s (now widely distributed—Colbert, 1989) continue to be prepared, yielding many of the fossils listed in the following paragraphs. The most recent faunal review was by Rinehart et al. (2009), and diverse aspects of the taxonomy and paleobiology of *Coelophysis bauri* continue to be the focus of much research (e.g., Paul, 1993; Smith, 1997; Hunt et al., 1998a; Downs, 2000; Carpenter, 2002; Rayfield, 2005; Smith and Merrill, 2005; Nesbitt et al., 2006; Rinehart et al., 2007, 2009; Spielmann et al., 2007a). Of course, these fossils are the basis for character discrimination in *Coelophysis* in almost every phylogenetic analysis of Theropoda, of which there are far too many to profitably cite. The taphonomy of the quarry remains a topic of interest as well (Schwartz and Gillette, 1994; Rinehart et al., 2009).

Other than Hunt and Lucas (1993a), Long and Murry (1995) and Rinehart et al. (2009) have summarized the known fauna of the Whitaker quarry. Updates include the description of *Hesperosuchus* from the quarry (Clark et al., 2001), the presence of a drepanosaurid (Harris and Downs, 2002; Renesto et al., 2010), the new sphenodontian *Whitakersaurus bermani* (Heckert et al., 2008); a spectacular skeleton of the archosauromorph *Vancleavea campi* (Hunt et al., 2002; Nesbitt et al., 2009b), a juvenile skull of the phytosaur *Redondasaurus* (Rinehart et al., 2009; Lucas et al., 2013), *Postosuchus* or a similar rauisuchian (Long and Murry, 1995; Novak, 2004), a shuvosaurid (holotype of *Effigia okeefae* Nesbitt and Norell, 2006, regarded as a synonym of *Shuvosaurus* by Lucas et al., 2007b; see also Nesbitt, 2007), and the rare theropod *Daemonosaurus chauliodus* Sues et al. (2011).

South-central New Mexico

Although Triassic vertebrate fossils were originally reported from Upper Triassic strata in south-central New Mexico (specifically Socorro County) by Case (1916), to date these outcrops have yet to yield major discoveries, and even identifiable vertebrate fossil remains are rare. Strata in this region include outcrop belts to the east and southeast of Socorro near Carthage (Fig. 3) as well as in the Lucero uplift to the northwest of Socorro; the Chinle outcrops farther to the east in Lincoln County are not known to be fossiliferous (Lucas, 1991). Spielmann and Lucas (2009) recently reviewed the record of Socorro County and we draw heavily upon that review for this summary.

Socorro County/Carthage—Upper Triassic stratigraphic units recognized in this region by Spielmann and Lucas (2009; following Lucas, 1991) are the Shinarump and San Pedro Arroyo formations, the latter divided into the Arraya Well (lower), Ojo Huelos (middle), and Cañon Agua Buena (upper) members (Fig. 4). To date, the Arraya Well Member has yielded only fragments of unidentifiable archosauriform reptiles (Spielmann and Lucas, 2009), so the bulk of the known fauna was derived from the Ojo Huelos and Cañon Agua Buena members.

Lucas (1991), Heckert (2001, 2004) and Heckert and Lucas (2002a) all described vertebrates, including some microvertebrates, from the Ojo Huelos Member, some of which were illustrated by Heckert et al. (2007a) as well. The most productive locality yields extremely small teeth of *Lonchidion* (=*Lissodus*) *humblei*, other, indeterminate chondrichthyans, various actinopterygians, including both redfieldiids and semionotids, possible coelacanthids, fragmentary temnospondyls, and indeterminate reptiles, as well as numerous vertebrate coprolites

(Heckert and Lucas, 2002a; Heckert, 2004; Heckert et al., 2007a). Other Ojo Huelos Member localities yield additional, fragmentary remains of metoposaurid temnospondyls and archosauriforms, principally phytosaurs (Spielmann and Lucas, 2009).

As reported by Spielmann and Lucas (2009), the Triassic fossils reported by Case (1916) appear to have been derived from above the Ojo Huelos Member in the Cañon Agua Buena Member. The assemblage consists primarily of indeterminate phytosaurs and other archosauriform reptiles.

Lucero uplift—The Lucero uplift, on the western margin of central New Mexico, superficially appears extremely promising as a potential place to prospect for Triassic vertebrates based on its extensive mapped area of Triassic deposits. Unfortunately, most of these "outcrops" are, in fact, covered intervals of reddish soils developed on Chinle and Moenkopi rocks (Lucas and Hayden, 1989), and structural complexities further hinder collecting efforts. A few fragmentary fossils are known from the western portion of the uplift (Lucas and Heckert, 1994; Heckert, 1997a, 1999; Zeigler et al., 2002b). An osteoderm from the San Pedro Arroyo Formation was identified as *Desmatosuchus* by Lucas and Heckert (1994). Heckert (1997a, 1999) described an incomplete pelvis and other postcrania of an associated phytosaur skeleton from the Bluewater Creek Formation he assigned to *Rutiodon*, noting similarities to the type of *Smilosuchus gregorii,* but choosing to retain the species in *Rutiodon*. Because existing taxonomic schemes for phytosaurs (e.g., Stocker and Butler, 2013) all but ignore the postcrania, and even the lower jaw, it is difficult to identify specimens such as this, but we note that the morphology of this specimen is consistent with that of the holotype of *Smilosuchus gregorii* (Long and Murry, 1995). The ilium is also similar to that of the holotype of "*Machaeroprosopus*" *zunii* illustrated by Stocker and Butler (2013, fig. 4c).

Other Bluewater Creek Formation localities in the Lucero uplift have yielded the lungfish *Arganodus*, metoposaurid amphibians pertaining to both a larger taxon (*Koskinonodon*?) and *Apachesaurus*, as well as indeterminate cranial and postcranial bones of archosauriforms, principally phytosaurs and aetosaurs (Heckert, 1999; Zeigler et al., 2002b).

Central New Mexico

For the Upper Triassic vertebrate paleontology around the Sandia uplift (Bernalillo County) and in Santa Fe County, key citations include Lucas and Heckert (1995) and Hunt and Lucas (1995). The outcrops in Santa Fe County near Lamy are locally extremely fossiliferous and, among other things, include the famous Lamy amphibian (metoposaur) mass death assemblage first discussed in print by Romer (1939).

Santa Rosa Formation, Los Esteros Member—Hunt and Lucas (1988, 1995) reviewed an extensive assemblage of fossil vertebrates from the Los Esteros Member of the Santa Rosa Formation collected south of Lamy in Santa Fe County. This assemblage is the type assemblage of the Lamyan sub-faunachron of the Adamanian lvf (Hunt et al., 2005). It includes the holotypes of *Krzyzanowskisaurus hunti* (Heckert, 2002), and *Typothorax antiquum* Lucas et al. (2002a), and also encompasses a lungfish (*Arganodus*), redfieldiid fishes and cf. *Turseodus*, both large and small metoposaurids (*Koskinonodon* and *Apachesaurus*), *Trilophosaurus*, phytosaurs (including a partial skull of *Angistorhinus* described by Hunt et al., 1993b), other aetosaurs, a shuvosaurid and other rauisuchians, dinosaurs?, and a dicynodont femur that Lucas and Hunt (1993b) referred to cf. *Ischigualastia*. Recently, Kammerer et al. (2013) re-identified the dicynodont femur as pertaining to a kannemeyeriiform similar to *Stahleckeria*, but distinct from *Placerias*, and not identifiable below that level. Most of the vertebrate fossils from the Los Esteros Member await more detailed descriptions.

Garita Creek Formation—The Garita Creek Formation in Santa Fe County is host to the famous Lamy amphibian quarry (e.g., Fig. 1D–E), but has also yielded additional assemblages of fossils. Particularly important are referred specimens of the aetosaur *Typothorax antiquum* Lucas et al. (2002a). Additional material has been referred to phytosaurs, rauisuchians and dinosaurs, but has not been described in detail (Hunt and Lucas, 1995).

Beginning in the late 2000s, the NMMNH received permission to re-access the Lamy amphibian quarry and has undertaken extensive excavations there, including excavating a block that dwarfs those on display at Harvard (Fig. 1E) or the Smithsonian. Based on these new excavations, Lucas et al. (2010; see also Hunt and Lucas, 1989, 1995) reinvestigated the taphonomy of the Lamy amphibian quarry, which had never been addressed other than informally when Romer (1939, p. 339) described it as the "last scene in a drama of drought," and by Zeigler et al. (2002e), who questioned the scenario envisioned by Romer. Lucas et al. (2010) documented that the monodominant assemblage has actually been transported and was deposited in a floodplain environment, but does consist almost entirely of metoposaurid amphibians currently assigned to *Koskinonodon perfectum*. The model favored by Lucas et al. (2010) is that an aggregation of large metoposaurids experienced catastrophic mortality (cause unknown) at a site distinct from the quarry, and was subsequently disarticulated and disassociated, with rapid transportation of the bones onto a floodplain where they were buried in fine-grained sediment that underwent pedogenesis.

East-central New Mexico

East-central New Mexico here refers to the single largest outcrop area of the Chinle Group in New Mexico—in the greater drainages of the Canadian and Pecos Rivers in San Miguel, Guadalupe and Quay Counties (Fig. 3). Little studied until the 1980s, this outcrop belt now yields the most extensive body fossil record of Chinle Group vertebrates in New Mexico. Lucas et al. (1985, 2001b) provided reviews of this record, but much research has been undertaken since the 2001 review.

Santa Rosa Formation—Only a few fragmentary metoposaurids are known from the Santa Rosa Formation in east-central New Mexico (Lucas et al., 2001b). This may largely reflect a lack of collecting effort in that unit.

Garita Creek Formation—Hunt et al. (1989) reported an assemblage of fragmentary fossils of lungfish (*Arganodus*), metoposaur, phytosaur, aetosaur (including possible *Desmatosuchus*), and rauisuchians from the Garita Creek Formation in east-central New Mexico. Given the abundance of vertebrates in this unit near Lamy, the sparse record from east-central New Mexico may largely reflect a lack of collecting effort in that unit.

Trujillo Formation—Although the Trujillo Formation consists primarily of coarse-grained sandstones, conglomeratic sandstones, and conglomerates, it has yielded a few vertebrate fossils in recent years. Some of these are osteoderms of the aetosaur *Typothorax coccinarum* and fragmentary fossils assigned to the phytosaur *Pseudopalatus* by Hunt (2001a). The Mesalands Dinosaur Museum in Tucumcari has sought to expand upon these collections, but to date their results remain unpublished.

Bull Canyon Formation—The vast majority of the body fossil record of the Upper Triassic in eastern New Mexico comes from the Bull Canyon Formation, which is exposed in broad badlands, especially in the vicinity of Barranca, Plaza Larga, and Revuelto creeks. These badlands were extensively collected by parties working for Hunt, whose dissertation (Hunt, 1994) followed shortly after the review by Hunt and Lucas (1993a). The faunal component of the dissertation was published as Hunt (2001b), and numerous projects in the Bull Canyon Formation based on these and other collections have been published since 1993 (Table 4). The Bull Canyon Formation assemblages constitute the characteristic ("type") assemblage of the Revueltian land-vertebrate faunachron (Lucas and Hunt, 1993a), and have been subdivided into Barrancan and Lucianoan faunachrons (e.g., Hunt, 2001b).

The most basal vertebrates in these assemblages are fishes and temnospondyls. Murry and Kirby (2002) named a new taxon, *Reticulodus synergus*, based on shark teeth from the Owl Rock Formation of Arizona, but also referred specimens from the Bull Canyon Formation to this taxon . Hunt (1997a) named a new coelacanth, *Quayia zideki,* based on a distinctive basisphenoid from the Revuelto Creek badlands. Another interesting occurrence is of three-dimensionally preserved osteichthyan skeletons from a locality in the Barranca badlands (Hunt, 2001a). The only other non-amniote that is common in the Bull Canyon Formation is the metoposaurid temnospondyl *Apachesaurus gregorii* Hunt (1993), known from many localities throughout the formation (Hunt, 2001b).

An especially significant discovery in the Bull Canyon Formation was of the oldest turtle fossils in North America. These were originally reported by Hunt (1994) and subsequently published by Lucas et al. (2000; Hunt, 2001b). After discovery of additional material, principally shell fragments, Joyce et al. (2009) named this taxon *Chinlechelys tenertesta* and demonstrated that it is of comparable age to other, better known Triassic turtles such as *Proganochelys* and *Proterochersis* from Germany and *Palaeochersis* from Argentina. It is not as old as *Odontochelys*, which was described at nearly the same time (Li et al., 2008—Joyce et al. was in press at the time). *Chinlechelys* is important as it documents that an intermediate stage of development in the turtle carapace is a complex composite in which the costals are only weakly fused to the ribs (Joyce et al., 2009).

The overwhelming majority of the vertebrate fossil record of the Bull Canyon Formation is of archosauromorphs, principally phytosaurs and aetosaurs, but also including an array of other taxa. Among the more basal taxa, interesting records include an exceptionally young (stratigraphically high) rhynchosaur assigned to *Otischalkia elderae* (Spielmann et al., 2013) and multiple occurrences of the enigmatic archosauriform *Vancleavea* (Long and Murry, 1995; Hunt et al., 2002; Nesbitt et al., 2009).

The taxonomy of phytosaurs from the Bull Canyon Formation was investigated by Long and Murry (1995) and Hunt (2001b). Hunt et al. (2006a) hypothesized sexual dimorphism in the large phytosaur skulls from the region, and Heckert et al. (2013) described several juvenile specimens from this and other units in New Mexico and Texas. Many of these specimens are now on display in the NMMNH Triassic hall. Recent revisions of phytosaurs have done little to stabilize the taxonomy, with Bull Canyon Formation specimens variously referred to *Pseudopalatus* (e.g., Hungerbühler, 2002; Hunt, 2001b; Lucas et al., 2001b, 2002a; Zeigler et al., 2002d), *Arribasuchus* (Long and Murry, 1995), and now, apparently, *Machaeroprosopus* as discussed previously with the holotype of "*Belodon*" *buceros* and the Painted Desert Member of north-central New Mexico (Parker et al., 2013; followed by Hungerbühler et al., 2013 and Stocker and Butler, 2013).

Aetosaurs and their close relative *Revueltosaurus* have received much attention. The occurrence of ornithischian-like *Revueltosaurus* teeth associated with a non-dinosaurian skull and postcrania in the Painted Desert Member of Arizona (Parker et al., 2005) was corroborated by finds in the Bull Canyon Formation by Hunt et al. (2005b). Heckert and Camp (2006; Heckert and Miller-Camp, 2013) also reported on the tooth enamel microstructure of this enigmatic taxon. Aetosaurs from the Bull Canyon Formation were published as new records of *Aetosaurus* (Heckert and Lucas, 1998; Hunt, 2001b), and spectacular articulated specimens of *Typothorax coccinarum* from both Revuelto Creek and the Barranca badlands are known (Hunt et al., 1993c; Hunt, 2001b; Heckert et al., 2010). Other specimens have been referred to *Paratypothorax* (Hunt, 2001b), a new species of *Desmatosuchus* (Hunt, 2001b) named *D. smalli* (Parker, 2005), and *Rioarribasuchus* (=*Desmatosuchus*) *chamaensis* (Zeigler et al., 2002a; Parker, 2007).

Other suchians remain poorly known, but include a variety of "rauisuchians," including *Postosuchus* (Long and Murry, 1995; Hunt, 2001b). Hunt et al. (2006b) described an enigmatic sphenosuchian from the unit. *Shuvosaurus inexpectatus* Chatterjee (1993) was first identified from the Bull Canyon Formation of Texas (and is a senior synonym of *Chatterjeea elegans* Long and Murry; Nesbitt and Norell, 2006; Nesbitt, 2007), but also occurs in New Mexico (Hunt, 2001b); it clearly is not an ornithomimosaur, as originally described by Chatterjee (Hunt et al., 1998a; Heckert and Lucas, 2000a), but in fact represents a suchian (e.g., Nesbitt et al., 2007). Numerous other fragmentary fossils of crocodile-line archosaurs are known from the Bull Canyon Formation, but the affinities of many remain enigmatic (Hunt, 2001b).

Dinosaur fossils remain rare in the Bull Canyon Formation. Carpenter (1997) published the large coelophysoid *Gojirasaurus quayi*, and Hunt et al. (1998a) described additional, fragmentary records of theropods from the unit (see also Hunt, 1994, 2001b). Nesbitt et al. (2007, p. 222) considered the holotype of *Gojirasaurus quayi* and various associated fossils to represent a chimaera including indeterminate dinosauriform fossils and material indistinguishable from *Shuvosaurus*, and restricted the holotype to the pubis and femur and assigned it to Coelophysoidea *incertae sedis*. The enigmatic taxon *Lucianosaurus wildi* Hunt and Lucas (1994) may not represent an ornithischian (Irmis et al., 2007b), but is still a distinct archosauriform. Hunt (1994, 2001b; see also Hunt et al., 1998a) considered other, fragmentary specimens to represent possible herrerasaurid dinosaurs, although these records were not considered diagnostic by Nesbitt et al. (2007) and were referred to as a "possible indeterminate saurischian" and "Archosauria indet." by those authors.

Redonda Formation—Although historical collections from the Redonda Formation extend back at least as far as Gregory (1957, 1972; Baird, 1964; Hunt, 1997b), the vast majority of the published records have occurred since Hunt and Lucas (1993a), and were most recently summarized by Spielmann and Lucas (2012; see also Spielmann et al., 2006a), upon which we draw heavily here. The Redonda Formation hosts the characteristic ("type") assemblage of the Apachean land-vertebrate faunachron of Lucas and Hunt (1993a).

In addition to numerous new publications on its fossil vertebrates, the Redonda Formation has undergone dramatic revision of its sedimentology and stratigraphy (e.g., Hunt and Lucas, 1997; Hester and Lucas, 2001; Lucas et al., 2001b, 2006b; Cleveland et al., 2007). In spite of its relatively localized outcrop areas, the Redonda Formation is remarkable for its preservation of both body and trace fossils, including articulated fish (Huber et al., 1993; Johnson et al., 2002; Milner et al., 2006), "typical" Chinle assemblages of temnospondyls (Hunt, 1993) and archosauromorphs (Heckert et al., 2001), a cynodont (Lucas et al., 1999a; Spielmann and Lucas, 2012), and abundant trace fossils. Like the body fossils, the trace fossils are remarkably diverse and include *bona fide* lungfish burrows (Gobetz et al., 2006) in addition to diverse tracks and trackways (Lockley and Hunt, 1995; Hunt and Lucas, 2007; Lucas et al., 2010b) and coprolites (e.g., Hunt et al., 1998b), all covered in more detail by Hunt and Lucas (2015) elsewhere in this volume.

Among the records reanalyzed and summarized by Spielmann and Lucas (2012) were a giant phytosaur skull and associated assemblage (Heckert et al., 2001; Spielmann et al., 2006a) and the records of the poorly known aetosaurs, especially *Redondasuchus*, for which Spielmann et al. (2006b) named the new species *Redondasuchus rineharti*. The validity of *Redondasuchus* has been questioned by some (e.g., Long and Murry, 1995) but recognized as, minimally, a valid species (of *Typothorax*—see Martz, 2002). Heckert et al. (2010) found no osteoderms matching those of the holotype in essentially complete carapaces of *Typothorax coccinarum*. *Redondasuchus* is therefore generally treated as a valid, if poorly known and somewhat problematic, taxon (Parker, 2007; Desojo et al., 2013). Spielmann and Lucas (2012) also named a new genus and species, *Apachesuchus heckerti*, based on several osteoderms that almost completely lack ornamentation that were first described by Heckert et al. (2001), who considered them extremely similar to those of *Neoaetosauroides* from the Upper Triassic of South America (e.g., Heckert and Lucas, 2000b).

As with *Redondasuchus*, the phytosaur *Redondasaurus* has been synonymized with other, older taxa (e.g., *Pseudopalatus*—Long and Murry, 1995), although others have recovered it as a distinct taxon (Hungerbühler, 2002; Parker and Irmis, 2006); Stocker and Butler (2012) listed it as a distinct genus. Spielmann and Lucas (2012) extensively reviewed *Redondasaurus*, identifying diverse new diagnostic characters, further validating the genus. More recently, Hungerbühler et al. (2013) followed Parker's (2013) resurrection of the generic name *Machaeroprosopus* for some Chinle phytosaurs, and considered the genus *Redondasaurus* a junior synonym of *Machaeroprosopus* on cladistic grounds. However, they (Hungerbühler et al., 2013) did recognize "*R.*" *bermani* as a distinct species.

Northeastern New Mexico

In northeastern New Mexico, the Dry Cimarron drainage contains Triassic outcrops assigned by Lucas et al. (1987; Lucas, 2004) to the Baldy Hill, Travesser, Sloan Canyon, and Sheep Pen formations, in ascending order (Fig. 4). The majority of Triassic fossils in this region are footprints from a variety of tracksites, some of which have long been known (e.g., Baird, 1964; Conrad et al., 1987); relatively few body fossil localities are known. Tracksites occur primarily in the Sheep Pen Formation, but others are known from the Travesser and Sloan Canyon formations (Lockley et al., 1993; Lockley and Hunt, 1995, 1996) and are covered separately by Hunt and Lucas (2015) in this volume.

Since Hunt and Lucas (1993a), relatively little has been published directly on the Triassic vertebrate paleontology of this region of New Mexico. The Cobert Canyon beds at the top of the Baldy Hill Formation are interpreted here as the base of the Chinle. Fossils from this unit here (Lucas et al., 1987) and in southeastern Colorado (Heckert et al., 2012c), are fragmentary but typical Chinle fossils of temnospondyls (probably metoposaurs), phytosaurs, and aetosaurs. A microvertebrate assemblage from the Sloan Canyon Formation (Hunt and Lucas, 1993e; Heckert et al., 2002) is under study; small sharks pertaining to *Lonchidion* from this site were mentioned by Heckert et al. (2007a). The Travesser Formation phytosaur skull originally described by Stovall and Savage (1939) was assigned to *Redondasaurus* by Hunt and Lucas (1993c; see also Spielmann and Lucas, 2012). Heckert et al. (2013) described a juvenile phytosaur mandible from the Travesser Formation as well. Otherwise, the known vertebrate fauna from the unit largely comprises the fossils described by Lucas et al. (1987) and last reviewed in context with the Redonda Formation assemblages described by Spielmann and Lucas (2012).

VERTEBRATE-TRACE-FOSSIL PALEONTOLOGY OF THE CHINLE GROUP

Numerically, coprolites dominate the Late Triassic, vertebrate

trace fossil record of New Mexico because they are known from many bone-bearing localities (Hunt et al., 1998b, 2007). Vertebrate tracks are less commonly recovered than vertebrate body fossils throughout most of New Mexico; the only possible exception being the Redonda Formation in eastern New Mexico and other uppermost Chinle units in northeastern New Mexico. Other traces include occasional vertebrate bite marks (e.g., Heckert et al., 2001; Rinehart et al., 2008). Hunt and Lucas (2015), in this volume, provide a review of the Triassic vertebrate trace fossil record in New Mexico.

SIGNIFICANCE

Some of the first Triassic vertebrates known from the American Southwest were found in New Mexico (Cope, 1875a,b, 1877, 1881). Subsequent study was somewhat halting and intermittent (see reviews by Long et al., 1989 and Long and Murry, 1995), but generated important collections, including not only many holotypes, but also large sample sizes from major bonebeds (e.g., the Canjilon, Lamy, and Whitaker quarries). After decades in which there was seldom more than one researcher engaged in field work, now is a "golden age" of studies of the Triassic vertebrates of New Mexico, with major ongoing efforts by numerous personnel from multiple institutions and, if the backlog of jackets awaiting preparation is any indication, many discoveries soon to come.

Within the framework of the Moenkopi and Chinle lithosomes, several aspects of the Triassic record of New Mexico stand out. These include its stratigraphic coverage, combinations of body and trace fossil records, bonebeds that yield especially large samples, the diversity of taxa (especially tetrapods), and evolutionarily important records, such as early dinosaurs and North America's oldest turtle. These thus have major implications for our understanding of the paleobiology of many taxa, in many cases providing unique insights. We briefly summarize all of these facets for the Moenkopi Formation before providing a series of summaries of the stratigraphic and paleobiological significance of New Mexico's Chinle vertebrates.

Global Significance of Moenkopi Formation Vertebrates from New Mexico

Although Moenkopi strata in New Mexico are only comparable to the uppermost part of the lithosome in Arizona, and lack equivalents to the Wupatki and Moqui members, they still preserve diverse assemblages as documented here. Ongoing exploration should help bridge the gap between the known fauna and that of the correlative Holbrook Member in Arizona (e.g., Heckert et al., 2005b; Nesbitt, 2005). The temnospondyls from this interval are much of the basis of the Perovkan lvf and provide important ties to other units, such as the upper Buntsandstein of Germany (Lucas and Schoch, 2002). Preparation of the large collections at the NMMNH from the monospecific Anton Chico bonebed will doubtless shed light on the paleobiology of that capitosaurid because it appears capable of yielding literally dozens of skulls. Moreover, the bonebed has yielded the first complete postcranium of *Eocyclotosaurus*, which consists of bones of many individuals of various ontogenetic stages, so the postcranial anatomy and ontogeny of this capitosaur will be documented for the first time.

Upper Triassic Biostratigraphy and Biochronology

Lucas and Hunt (1993a) erected a four-fold biochronologic subdivision of the Late Triassic of North America based on the biostratigraphic superposition of four assemblages across the Chinle lithosome (e.g., Lucas, 1993, 1997). These were termed the Otischalkian, Adamanian, Revueltian, and Apachean (Fig. 4), and have been extended to usage throughout the American West and, to the extent possible, globally (e.g., Lucas, 1998, 2010). Various parties have sought to subdivide and/or modify the lvf scheme (e.g., Hunt, 2001b; Hunt et al., 2005; Heckert and Lucas, 2006; Lucas et al., 2007c), and much ink has been spilt debating the merits of the lvfs locally (Long and Murry, 1995) and globally (e.g., Irmis et al., 2010). Nevertheless, almost all workers, even vehement critics, recognize that the FADs of key taxa occur in the expected order in Texas (e.g., Martz, 2008), New Mexico, and Arizona (e.g., Parker and Martz, 2011). Importantly, most "challenges" to the biochrons occur exactly where pre-existing stratigraphic hypotheses would predict. One example is the Adamanian/Revueltian turnover in the Sonsela Member (Parker and Martz, 2011), which Heckert and Lucas (2002b) noted was much thicker and more fossiliferous than previously thought. Another may be in the Owl Rock Formation interval, which is unambiguously above the Painted Desert Member. To thoroughly review the history of debate is beyond the scope of this review, but, given that the characteristic or "type" assemblages of the Revuletian and Apachaean lvfs occur in east-central New Mexico, we highlight our current understanding of those assemblages here (Table 4).

The Bull Canyon Formation of east-central New Mexico yields the characteristic assemblage of the Revueltian, named for the badlands around Revuelto Creek. Since a review of this assemblage by Hunt (2001), relatively little has changed other than the perceived nomenclature of the phytosaurs (but not their stratigraphic distribution; see below). Key additions include the identification of the Bull Canyon Formation hybodont as *Reticulodus synergus* (Murry and Kirby, 2002), the stratigraphically youngest rhynchosaur (Spielmann et al., 2013), the Barranca Creek skeleton of *Typothorax coccinarum* (Heckert et al., 2010), and updates on one of the sphenosuchians (Hunt et al., 2006b).

Regardless of the generic assignments of phytosaurs by various authors (e.g., Long and Murry, 1995; Hunt, 2001a; Lucas et al., 2002a; Parker et al., 2013; Hungerbühler et al., 2013) to *Pseudopalatus*, *Nicrosaurus*, *Machaeroprosopus*, and *Arribasuchus*, the species "*buceros*" is an index fossil of the Revueltian and widely known from other regions lithostratigraphically correlated to the Bull Canyon Formation (e.g., Painted Desert Member of Chama basin and Arizona, especially the Petrified Forest National Park, Bull Canyon Formation of Texas; Lucas, 1993, 1997). Similarly, the aetosaur *Typothorax coccinarum* has a nearly identical stratigraphic distribution. Both taxa are found as high stratigraphically as the Owl Rock Formation in Arizona (e.g., Long and Murry, 1995; Spielmann et al., 2007b; Table 4). Table 4 indicates our current understanding of the Bull Canyon Formation assemblage and thus the characteristic Revueltian assemblage.

Spielmann and Lucas (2012) recently reviewed the Apachean characteristic vertebrate assemblage from the Redonda Formation in east-central New Mexico, so we only reiterate a few points here. These include that, following Heckert et al. (2010), Spielmann and Lucas (2012) could not find convincing evidence for a large-bodied aetosaur other than *Redondasuchus* from the Redonda Formation—no published material from the unit can be referred to *Typothorax coccinarum* or any other taxon. Similarly, *Apachesuchus heckerti*, while not well known, is clearly distinct from the recently named *Stenomyti huangae* Small and Martz (2013). Even if one does not accept the hypothesis of sexual dimorphism in phytosaurs, both nominal species of *Redondasaurus* (*R. gregorii* and *R. bermani*, both recognized as valid by Stocker and Butler, 2013) are restricted to uppermost Triassic strata not just in the type area, but also in northeastern New Mexico and southern Utah (e.g., Lucas et al., 2011). Table 4 indicates our current understanding of the Redonda Formation assemblages of eastern New Mexico, and therefore the characteristic Apachean assemblage.

New Mexico's Contributions to Late Triassic Vertebrate Paleobiology

Paleobiological inferences based on extinct taxa are more robust if bolstered by a rich fossil record. Triassic bonebeds in New Mexico provide several opportunities to investigate taxa preserved in large numbers, including at least two cases where the minimum number of individuals (MNI) exceeds 50—the Lamy bonebed, which has yielded dozens of skulls of the metoposaurid *Koskinonodon* (e.g., Colbert and Imbrie, 1956), and the Whitaker quarry at Ghost Ranch, with a minimum of several hundred individuals of *Coelophysis* preserved, of which up to 70 are complete enough to include in a range of statistical analyses (Rinehart et al., 2009) (Fig. 6). The rich, Revueltian-age Hayden, Snyder, and Canjilon quarries also produce numerous individuals of some taxa, especially phytosaurs (more than ten skulls known from both the Canjilon and Snyder quarries). To emphasize the importance of these assemblages, we reiterate some of the key conclusions we and others have drawn from them in recent years.

Both the Canjilon and Snyder quarries, which lie at or near the same stratigraphic level in the Painted Desert Member, yield numerous skulls of the phytosaur *Pseudopalatus* ("*Machaeroprosopus*" to some) *buceros*. The large sample collected by UCMP crews working for C.L. Camp at the Canjilon quarry was used by Zeigler et al. (2002c, 2003f) as a basis for postulated sexual dimorphism, with males possessing a well-developed narial crest constructed by the septomaxillae and nasals, whereas females have the uncrested, superficially more gracile snout. Although questioned by some (e.g., Stocker, 2010), who have not always recovered sister-group relationships between putative dimorphs of other phytosaurs, the most recent review (Stocker and Butler, 2013) does allow for dimorphs in *P. buceros* and other pseudopalatines based on both co-occurrences, such as those at the Snyder and Canjilon

TABLE 4. Vertebrate fauna of the Upper Triassic Bull Canyon and Redonda formations of eastern New Mexico. Binomens with author(s) indicate type specimens.

Bull Canyon Formation
(characteristic Revueltian assemblage)
(updated from Hunt, 2001b)
Chondrichthyes
Reticulodus synergus Murry and Kirby 2002; R
Osteichthyes
Actinopterygii indet.
Redfieldiidae indet.
Coealacanthidae indet.
Quayia zideki Hunt 1997a; R

Amphibia
Metoposauridae
Apachesaurus gregorii Hunt 1993
Apachesaurus sp.
Reptilia
Chinlechelys tenertesta Joyce et al. 2008; R

Diapsida
Archosauromorpha indet.
Otischalkia elderae
Archosauriformes indet.
Vancleavea campi
Phytosauria indet.
Machaeroprosopus buceros
Nicrosaurus/Arribasuchus/
Pseudopalatus spp.
Revueltosaurus callenderi Hunt, 1989; R
Stagonolepididae indet.
Typothorax coccinarum R
Aetosaurus sp.
Desmatosuchus sp.
Paratypothorax sp.
Rioarribasuchus sp.
Sphenosuchidae indet.
Gojirasaurus quayi Carpenter, 1997
Theropoda indet.

Redonda Formation
(characteristic Apachean assemblage)
(after Spielmann & Lucas, 2012)
Osteichthyes
Actinopterygii indet.
Redfieldiidae indet.
Palaeoniscidae indet.
Semionotus sp.
Hemicalypterus sp.
Synorichthys sp.
Synorichthys stewarti
Coelacanthidae indet.
Amphibia
Metoposauridae
Apachesaurus gregorii
Apachesaurus sp.
Reptilia
Synapsida
Redondagnathus quayi Spielmann and Lucas 2012; A
Diapsida
Archosauromorpha indet.
Archosauriformes indet.
Vancleavea campi
Phytosauria indet.
Redondasaurus gregorii A
Stagonolepididae indet.
Redondasuchus reseri Hunt and Lucas 1991; A
Redondasuchus rineharti Spielmann et al. 2006a; A
Apachesuchus heckerti A
Sphenosuchidae indet.
Redondavenator quayensis A

R = taxon known solely from the Revueltian; A = taxon known solely from the Apachean

quarries and the sister-taxon relationships of putative "species" of crested and uncrested morphs.

Rinehart et al. (2009) strove to untangle much of the paleobiology of *Coelophysis*, returning to past studies of cannibalism (Colbert, 1989; Nesbitt et al., 2006; see also Gay, 2010), dimorphism (Colbert, 1989, 1990), and taphonomy (e.g., Schwartz and Gillette, 1994), as well as more novel topics, such as vision in *Coelophysis*. Based on their own and previous analyses, Rinehart et al. (2009) concluded that:

—The bonebed represents a catastrophic accumulation of a large flock of *Coelophysis* individuals that were drowned and buried by a sheet flood event.

—*Coelophysis* was not only fast and agile, but a diurnal, visually oriented hunter with similar visual acuity, power of accommodation, and depth perception as modern-day avian raptors.

—*Coelophysis* grew rapidly, and that several age classes are represented in the assemblage (Fig. 6).

—The flock consists of approximately 20 yearlings and young juveniles per large adult, with sexual maturity occurring between years 2–3 and the oldest individuals being approximately seven (or more) years old (Fig. 6B).

—There is substantial evidence of sexual dimorphism, principally in the skull and neck (with one shorter, more robust morph) as well as in the sacrum and pelvis (Fig. 6A).

Although accepting that the one small individual posited to be within the rib cage of an adult was not a victim of cannibalism (Gay, 2002, 2010; Nesbitt et al., 2006), close examination of the matrix surrounding skulls in the *Coelophysis* block reveal that it is altered with what Rinehart et al. (2009) have interpreted as regurgitalites, some of which bear carpal elements indistinguishable from juveniles of *Coelophysis* and therefore provide compelling evidence of cannibalism.

New Mexico and the Rise of Dinosaurs

More than any other western state, New Mexico has contributed to our knowledge of Triassic dinosaurs. Beyond the Whitaker quarry sample of *Coelophysis* summarized previously and the original materials described by Cope (e.g., Sullivan et al., 1996), the state yields rich records of theropod dinosaurs from other localities (Carpenter, 1997; Heckert et al., 2000a,b, 2003; Hunt, 2001b; Spielmann et al., 2007a; see review by Nesbitt et al., 2007). Although the putative ornithischian *Revueltosaurus* was revealed to be a suchian archosaur (Parker et al., 2005), and other "ornithischian" records may only reflect indeterminate archosauriforms (Irmis et al., 2007b), ongoing discoveries continue to reveal numerous new dinosauromorph taxa, including early saurischians (e.g., Irmis et al., 2007a; Nesbitt et al., 2009a; Sues et al., 2011).

CONCLUSIONS

The record of fossil Triassic vertebrates from New Mexico is the most comprehensive and historically significant in the American West, and is globally important. In addition to its long historical record of study, the sheer wealth of diverse vertebrate fossils recovered from a wide range of stratigraphic units, including both body and trace fossils, is unmatched. Although efforts in the Moenkopi Formation have a century less history than do those of the Chinle, the pace of discovery there is high, and bonebeds in both the Moenkopi and Chinle provide abundant opportunities to describe diverse faunas and investigate variation in some taxa. Stratigraphically, the greatest strength of the Upper Triassic records in the state lies in the upper part of the Chinle

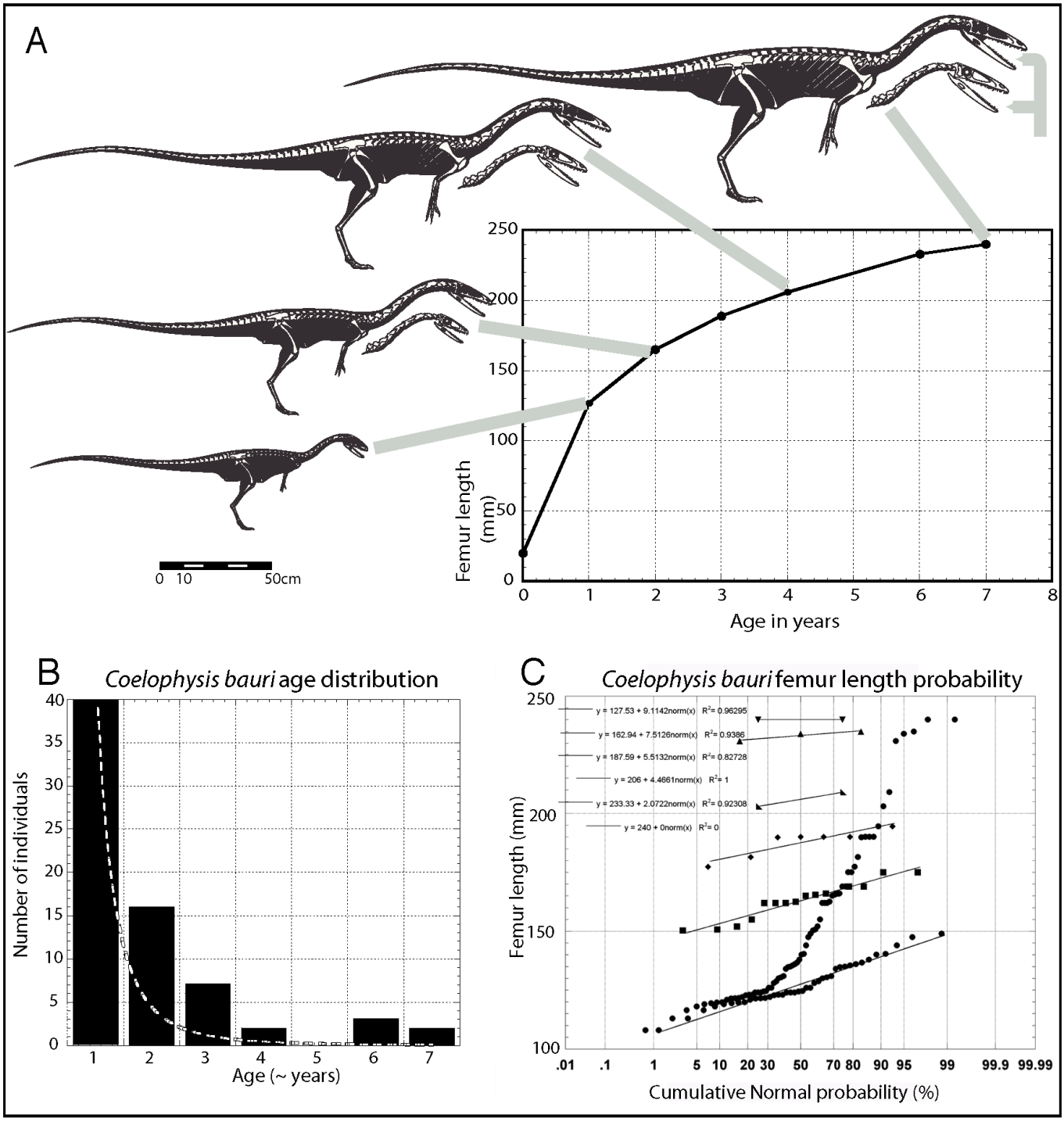

FIGURE 6. Paleobiology of *Coelophysis bauri* from the Whitaker quarry at Ghost Ranch, New Mexico. **A**, *Coelophysis bauri* hypothetical growth curve and skeletal reconstructions showing growth and onset of sexual dimorphism, modified from the cover and resolved age classes of Rinehart et al. (2009); **B**, age distribution of 70 individuals of *Coelophysis bauri* from the Whitaker quarry (data from Rinehart et al., 2009, table 6), the hyperbolic shape shows high juvenile mortality but reasonable expectation of long life after achieving age 2; and **C**, probability plot of femur length showing six resolved age classes that are the basis for A–B (after Rinehart et al., 2009, fig. 97b). Skeletal reconstructions by Matt Celeskey.

section. Revueltian assemblages are especially well known, not just from the type area at Revuelto Creek, but nearby badlands in east-central New Mexico and in the Chama Basin. Importantly, even though these collecting areas have long been known, it is increasingly clear that many exciting discoveries remain to be made. To wit, Hunt (2001b) only began to document the diversity of the Barranca badlands, an area that was largely inaccessible before the 1980s. Similarly, specimens described by Heckert et al. (2010) include those exposed in the immediate vicinity of localities discovered within a few years of the seminal dissertation by Hunt (1994, 2001b), demonstrating that none of these areas are likely to be "played out" anytime soon. With hundreds of jackets awaiting preparation and millions of acres of badlands continuously weathering, the next century of discoveries threatens to rival the last.

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